Characteristics of an Intergeneric Cyprinid Hybrid, *Campostoma anomalum* x *Luxilus* sp. indet. (Pisces: Cyprinidae), from the Portage River, Ohio[1]

William J. Poly, Department of Zoology, Southern Illinois University, Carbondale, IL 62901

Abstract. Characteristics of a hybrid, *Campostoma anomalum pullum* x *Luxilus* sp. (*chrysocephalus*, *cornutus*, their hybrid, or a backcross) from the Portage River, OH, were examined and compared with parental species as well as five other *Campostoma anomalum* x *Luxilus cornutus* and *C. anomalum* x *L. chrysocephalus* hybrids from Ohio, Tennessee, New York, Virginia, and Mississippi. Lateral-line scale count and gill raker count were consistently intermediate in all hybrids. Dentition was intermediate in four of five hybrids, and intestinal diameter was intermediate in both Ohio hybrids. Hybrids for which data were available (n = 5) resembled *Luxilus* in lacking intestinal coiling around the swimbladder and in liver shape and position (n = 4). Mouth position was intermediate in five of six hybrids. The Portage River hybrid may be a tri-hybrid based on apparent hybridization between the two *Luxilus* species, *L. cornutus* and *L. chrysocephalus*, present at the collection site.

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INTRODUCTION

Many natural hybrid combinations among cyprinids have been documented (Schwartz 1972, 1981). Cyprinid hybrids often result from accidental mixing of gametes during spawning due to nest "sharing" by several species. Species of non-nest building cyprinids often spawn over the nests of *Nocomis*, *Campostoma*, *Exoglossum*, or *Semotilus* (Raney 1940, 1947), and Thoma and Rankin (1988) found the incidence of *Luxilus chrysocephalus* (striped shiner) x *Notropis rubellus* (rosyface shiner) hybrids in Ohio streams strongly correlated with the presence of either *Nocomis biguttatus* (hornyhead chub) or *N. micropogon* (river chub). Trautman (1981) recorded the hybrid combinations *Campostoma anomalum* (stoneroller) x *L. cornutus* (common shiner) and *C. anomalum* x *L. chrysocephalus* from Ohio; however, character descriptions were not provided for these hybrids. Characters of a *C. a. pullum* x *L. cornutus* (UMMZ 121844) collected in Lost Creek, Defiance County, OH on 30 May 1938 by M. B. Trautman and G. A. Moore were examined and included herein. Menzel (1978) analyzed characters of a *C. a. pullum* x *L. cornutus* (CU 64399) from Sixmile Creek, Tompkins County, NY, and Grady and Cashner (1988) described the characteristics of a *C. a. pullum* x *L. chrysocephalus isolepis* (UNOVC 5336) from Clark Creek, Wilkinson County, MS. A hybrid *Campostoma anomalum pullum* x *Luxilus chrysocephalus/cornutus* was captured 13 July 1994 in the Portage River (PR), Lake Erie Drainage, at Pemberville, OH (Freedom Township, Wood County) by Ohio Environmental Protection Agency (OEPA) personnel (R. J. Miltner, K. M. Capuzzi, and W. J. Poly). The hybrid specimen (UT 44.6648) was preserved along with a series of each suspected parental species (UT 44.6646, UT 44.6647). The site was seined by the author on 23 May 1995 in search of more hybrids; however, none were captured. Also, two specimens of *C. a. anomalum* x *L. chrysocephalus* from Bletcher's Creek, Anderson County, TN and Bear Creek, Smyth County, VA (UT 44.3017 and UT 44.5785, respectively) were collected (D. A. Etnier, Univ. Tenn. pers. comm.) and included in the present study.

Hybrids often exhibit a combination of intermediacy and mosaic parental traits (Menzel 1978, Greenfield et al. 1973, Grady and Cashner 1988). Because the range of character variation in intergeneric hybrids can be even more extreme than the ranges of both parental species combined (Hubbs and Strawn 1957, Retzer and Walsh 1982, Grady and Cashner 1988), the characteristics of one hybrid specimen are not necessarily representative of even a typical hybrid of any given hybrid combination. In order to contribute additional information on natural hybrids, I compared characteristics of six *C. anomalum* x *L.* spp. with putative parental taxa.

MATERIALS AND METHODS

Twelve meristic, eleven morphometric (ten external, one internal), and several qualitative characters were examined and compared among the hybrids and parental species (n = 11 *C. a. pullum* and *Luxilus* sp. from the Portage River taken with hybrid on 13 July 1994). Data for the New York and Mississippi hybrids were taken from Menzel (1978) and Grady and Cashner (1988), respectively. Counts and measurements follow Hubbs and Lagler (1958). External measurements were made to the nearest mm with dividers. Morphometrics are expressed as percentage of standard length or head length. Intestine diameter was measured to the nearest 0.1 mm with dial calipers (mean of three measurements per fish). Chin pigmentation and anterior dorso-lateral scale counts (fifth scale row above lateral line) follow Gilbert (1964). Head length excluded the opercular membrane. Lateral scale size and shape were determined from scales taken one scale row above the lateral line below the dorsal fin insertion. Jaw osteology and vertebrae were visualized

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with the use of soft x-rays (3A, 30 mv, 15 sec.). Data for each character were compared qualitatively among the hybrids and parental taxa. The following abbreviations are used in the text and Table 1: anterior dorso-lateral scales (ADLS), circumferential scales (CS), lateral line (LL), lateral-line scales (LLS), chin pigmentation (CP), back

TABLE 1

Characteristics of a hybrid, Campostoma a. pullum *x* Luxilus *sp. indet., and parental species from the Portage River, OH (PR) and five additional* C. anomalum *x* L. *sp. hybrids from Mississippi (MS), Lost Creek, OH (LC), Tennessee (TN), Virginia (VA), and New York (NY). Mean count or measurement is given between the range which is in parentheses.*

Character	*Campostoma anomalum pullum* (n = 11)	Hybrids[§] (n = 6) TN	VA	PR	NY	MS	LC	*Luxilus* sp.* (n = 11)
Standard length (SL, mm)	(66)84(98)	45	66	111	87.0	48.0	78	(76)91(109)
Meristics								
Anal fin rays	(6)7(7)	8	8	7	8	8	8	(8)9(10)
Dorsal fin rays	(7)8(8)	8	8	8	–	–	8	8
Principal caudal fin rays	19	20	19	20	–	–	19	19
Pelvic fin rays (left)	(7)8(8)	8	8	8	–	–	8	(8)8(9)
(right)	8	8	8	8	–	–	8	(8)8(9)
Pectoral fin rays (left)	(16)17(17)	16	17	16	–	–	17	(15)15(17)
(right)	(16)16(17)	17	16	15	–	–	17	(15)16(17)
Lateral line scales	(49)52(54)	45	45	44	46	43	47	(38)39(40)
Scales above lateral line	(7)8(9)	7	7	8	–	–	8	(8)8(9)
Scales below lateral line	(7)8(8)	7	7	7	–	–	7	(6)6(7)
Anterior dorso-lateral scales	(21)23(24)	17	–	17	22	19[‡]	20	(19)21(23)
Circumferential scales	(36)40(42)	31	31	34	36	30	39	(33)34(36)
Pharyngeal teeth (n = 5)	4-4	1,4-4,1	1,4-?	1,4-4,0	–	1,4-4,1	4-4	2,4-4,2[¶]
Gill rakers (left/right)[†]	(24)-(33)	14/14	14/14	16/14	–	15	15/14	(6)8(8)
Precaudal vertebrae**	(23)24(24)	22	–	22	–	–	23	(21)21(22)
Caudal vertebrae**	(14)17(18)	18	–	18	–	–	17	(18)18(19)
Morphometrics (% SL)								
Body depth	(24)25(26)	24	24	26	–	22.7	29	(28)30(32)
Caudal peduncle depth	(11)12(13)	11	11	11	–	–	12	(10)11(12)
Dorsal fin base	(9)11(12)	16	12	13	–	–	13	(10)12(14)
Dorsal fin height	(15)17(19)	27	21	17	–	–	21	(18)20(22)
Anal fin base	(8)9(9)	11	11	10	–	–	10	(10)12(14)
Anal fin height	(14)15(16)	20	17	13	–	–	17	(13)15(17)
Predorsal length	(52)53(54)	51	50	50	53.3	52.5	53	(48)50(52)
Head length (HL)	(24)25(26)	27	26	23	25.4	–	27	(24)25(26)
Orbit width (fleshy) (% HL)	(18)21(25)	25	26	23	25.2	–	20	(22)26(28)
Snout length (% HL)	(35)40(43)	33	35	38	38.2	–	35	(25)30(35)
Other								
Internal (n = 5)								
Premaxillary extended past dentary	present	present	–	present	–	–	present	absent
Intestine	coiled, long	–	"s–shaped," short	coiled, short	–	–	IM	"s–shaped," short
Diameter (mm)	(1.2)1.6(2.1)	–	–	(2.2)2.3(2.4)	–	–	(2.0)2.3(2.6)	(2.9)3.7(4.6)
Coiled around swimbladder	yes	no	no	no	no	–	no	no
Peritoneum	brown with black speckles or streaks	{brown with black speckles}		brown/ black	– –	– –	brown	black or with black speckles
Liver shape	1	2	2	2	–	–	IM	2
Liver position	1	3	3	2	–	–	2	2 or 3
External (n = 11)								
Dark band in dorsal fin	present	–	absent	faint	present	–	–	absent
Black basicaudal patch	present	–	absent	faint	present	–	–	absent
Caudal fin lobe (lower)	rounded	–	–	rounded	–	–	pointed	pointed
Caudal fin fork	shallow	–	–	IM	–	–	IM	deep
Lateral band (posterior)	absent	–	present	present	present	–	faint	present
Mid–dorsal stripe (predorsal)	absent	present	present	present	present	present	present	present
Complete lateral line	present	present	present	absent	–	–	present	present
Anterior lateral line curvature	NS	NS	NS	NS	–	–	NS	strongly curved
Elevated anterior lateral line scales	absent	absent	absent	present	–	–	present	present
Lateral scale size	"small"	IM	IM	IM	–	–	IM	"large"
Lateral scale shape	slightly higher than wide, circular	–	–	IM, ovoid	–	–	IM, ovoid	much higher than wide, ovoid
Mouth position	inferior	inferior	subterminal	subterminal	subterminal	subterminal	subterminal	terminal
Cartilaginous mandibular shelf	present	absent	PD	PD	PD	absent	PD	absent

[§]Data from this study (PR, LC, TN, and VA), Menzel (1978, NY), and Grady and Cashner (1988, MS). **Luxilus cornutus* x *L. chrysocephalus* hybrids or backcrosses. Dashes indicate that no data are available. [‡]Predorsal scale count from Grady and Cashner (1988). [¶]*Luxilus* counts from Trautman (1981). [†]Information on the PR hybrid provided by D. Etnier, *C. a. pullum* counts from Burr and Cashner (1983), and *Luxilus* counts from Grady and Cashner (1988). **Counts from n = 5 *Campostoma a. pullum* and n = 6 *Luxilus* sp. Liver shape: 1, globular and round; 2, a main body and several thin, elongate lobes. Liver position: 1, does not extend beyond pectoral fin posterior margin; 2, extends beyond pectoral fin posterior margin; 3, extends beyond pelvic fin insertion. IM = intermediate; NS = nearly straight; PD = partially developed.

pigmentation (BP), Tennessee (TN), Mississippi (MS), Virginia (VA), New York (NY), Portage River, OH (PR), and Lost Creek, OH (LC). Museum abbreviations are as follows: Cornell University (CU), University of Tennessee (UT), University of Michigan Museum of Zoology (UMMZ), and University of New Orleans Vertebrate Collections (UNOVC).

RESULTS AND DISCUSSION

Characters of the Portage River Hybrid

Characteristics of the PR hybrid were intermediate in some instances or resembled one of the parental species (Table 1, Fig. 1). *A. Luxilus cornutus* x *L. chrysocephalus* hybrid or backcross is displayed as the *Luxilus* parent in Figure 1; however, the actual *Luxilus* parent of the hybrid may be either *L. cornutus*, *L. chrysocephalus*, their hybrid, or a backcross (see below). The most informative meristic characters were LLS (44) and dentition (1,4-4,0), which were clearly intermediate in the hybrid. The LLS counts for Portage River *C. anomalum* (spp. *pullum*) were consistent with data in Trautman (1981) for northern Ohio populations (higher than for *C. a. anomalum*). Orbit width was intermediate in the hybrid when comparing mean values, although overlap occurred with both parental species. Lateral scale size and shape, mouth structure, intestine, and caudal fin fork were also intermediate in the hybrid. The hybrid exceeded the parental species with 20 principal caudal rays (19 for both parental species) and was unique in having an incomplete LL, 17 ADLS, and slightly shorter head length than both parental species. The hybrid was more similar to *C. a. pullum* in anal ray count, body depth, snout length, black dorsal fin band, black basicaudal patch, lower caudal lobe shape, anterior lateral line curvature, partially developed cartilaginous mandibular shelf, and jaw structure, but resembled *Luxilus* in vertebral counts, predorsal length, posterior lateral band, predorsal stripe, circumferential scales, elevated anterior lateral line scales, and liver shape and position.

The livers and their relative positions differ greatly between *Luxilus* and *Campostoma*. The liver of *Campostoma* was globular, relatively compact and did not extend beyond the pectoral fin posterior margin. The liver of *Luxilus* consisted of a globose body anteriorly with several slender lobes projecting posteriorly, as noted by Miller (1963, p. 23) for *L. cornutus*. The ventral lobe extended beyond the posterior margin of the pectoral fins or beyond the pelvic fin insertion in some cases. The hybrid's liver was more similar to that of *Luxilus* and extended beyond the pectoral fin posterior margin, but this organ and the entire gut appeared to be somewhat disorganized and possibly malformed in the hybrid. The hybrid's intestine was much shorter than that of *C. a. pullum*, but had several coils in the same pattern as the *Campostoma* intestine. The coils in the hybrid were not aligned closely as were the many coils in *Campostoma* and did not surround the swimbladder as in *Campostoma*. The diameter of the hybrid's intestine was intermediate between the smaller *C. a. pullum* intestine and the larger diameter *Luxilus* intestine (Table 1).

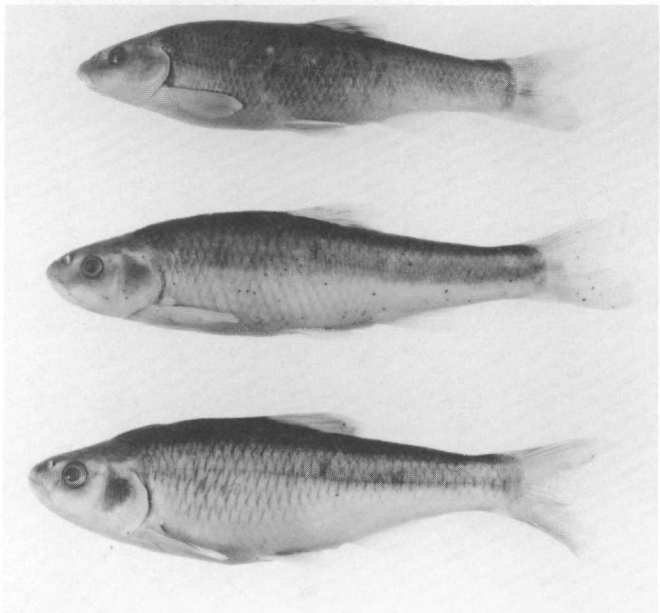

FIGURE 1. Lateral view (from top to bottom) of *Campostoma anomalum* (98 mm standard length), *Campostoma anomalum* x *Luxilus* sp. indet. (111 mm standard length), and *Luxilus cornutus* x *Luxilus chrysocephalus* hybrid or backcross (109 mm standard length). Photography by John Vercillo, Southern Illinois University.

Comparisons Among the Hybrids

Many of the scale counts would be expected to differ among the hybrids because the PR and NY hybrids' *Luxilus* parent possessed stronger *L. cornutus* characters, while the MS, TN, and VA hybrids' *Luxilus* parent, *L. chrysocephalus*, generally has lower scale counts than *L. cornutus*. Some characters are consistent among all the hybrids, while others vary to either parental extreme (Table 1). Pigmentation of the NY hybrid was nearly identical to that of the PR hybrid in that both possessed the same specific characteristics of both parents. All six hybrids had an intermediate number of lateral line scales (in parentheses): MS hybrid (43), PR hybrid (44), TN hybrid (45), VA hybrid (45), NY hybrid (46), and LC hybrid (47), intermediate mouth positions (except TN hybrid), and the dark middorsal stripe of the *Luxilus* parent. Gill raker counts on the first arch were intermediate in all hybrid specimens with data available. The NY, VA, LC and PR hybrids had a partially developed cartilaginous mandibular shelf that did not extend beyond the lower lip, whereas the MS and TN hybrids lacked this structure entirely. Dentition was intermediate in the PR, TN, VA, and MS hybrids, but the LC hybrid had a 4-4 count and resembled *C. a. pullum* in this regard. The NY hybrid was male, the PR hybrid was female, the LC hybrid appeared to be sterile, and the other hybrids were juveniles or subadults. Ovarian tissue with oocytes of various sizes (0.1 - 0.3 mm) was located in the anterior of the PR hybrid's abdominal cavity. Intestinal diameter and shape were typical for *Luxilus* in the VA hybrid. The author extracted food remains from portions of the gut of the VA hybrid and found 28 seeds, one chironomid, and one ephemeropteran.

Determination of the *Luxilus* Parent

Specific determination of the *Luxilus* parent of the PR hybrid may be impossible because it appears that *L. cornutus* and *L. chrysocephalus* have hybridized and possibly introgressed in the Portage River. Trautman (1981) noted that *L. cornutus* and *L. chrysocephalus* hybridize commonly in northern Ohio and recorded both species from the Portage River basin. The Portage River basin falls within the contact zone, an area with high incidence of hybridization between *L. chrysocephalus* and *L. cornutus* (Gilbert 1961, Dowling and Moore 1984). Hybridization also has been documented in the adjacent Maumee River basin (Dowling and Moore 1984). Dowling and Moore (1984) utilized principal component analysis, in part, to separate *L. cornutus*, *L. chrysocephalus* and their hybrids. Five characters contributing most to separation were LLS, CS, ADLS, CP, and BP.

In Portage River *Luxilus*, CP resembled *L. chrysocephalus* in two specimens, *L. cornutus* in five specimens, and was intermediate in four specimens. Dowling and Moore (1984) considered CP a good taxonomic character, but not a reliable indicator of hybridization. In all eleven individuals LLS were within the overlapping range for both species (38-40), while ADLS (19-23) and CS (33-36) were all clearly in the range of *L. cornutus*. BP was typical of *L. chrysocephalus* in all specimens (dark dorsal stripes converging to form "V's", Gilbert 1964). All of the *Luxilus* were considered hybrids or backcrosses based on intermediacy of the above parental characters. The Portage River may be a useful study area for future work concerning the *L. cornutus* – *L. chrysocephalus* relationship.

Although impossible to determine, the PR hybrid may be a tri-hybrid, (*L. cornutus* x *L. chrysocephalus*) x *C. a. pullum*, based on the apparent hybridization between the *Luxilus* spp. Tri-hybrids have been suspected among *Micropterus* spp. (Trautman 1981, p. 125) and among *Phoxinus* spp. and *Margariscus margarita* (pearl dace, Legendre 1970).

Probable Origin of the Portage River Hybrid

In addition to the hybrid, twenty-three species were captured at the hybrid site by OEPA personnel, and parental species abundance was 1,322 (*C. a. pullum*) and 67 (*Luxilus* sp.) (R. Miltner, OEPA pers. comm.). The substrate at the capture site consisted predominantly of cobble, gravel and bedrock. The presence of a considerable amount of bedrock may limit spawning habitat in this section of the river. Jenkins and Burkhead (1994) observed *L. chrysocephalus* reproductive activity over *C. a. anomalum* pits at two Virginia sites, and Raney (1940) noted *L. cornutus* use of *C. a. pullum* pit nests in New York. Gleason and Berra (1993) observed both *L. cornutus* and *L. chrysocephalus* breeding over *Campostoma* nests in Cedar Fork Creek, OH. Menzel (1978) concluded that the probable origin of the New York hybrid was excess *L. cornutus* milt washing downstream and fertilizing freshly extruded *C. a. pullum* eggs. Limited spawning habitat and the tendency for *L. cornutus* and *L. chrysocephalus* to utilize *Campostoma* nests may have contributed to the origin of the hybrid *C. a. pullum* x *L.* sp. described herein.

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